# THE ORIGIN AND BEHAVIOUR OF CHIASMATA

## VI. Hyacinthus amethystinus

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The original frequency and distribution and the later behaviour of chiasmata have been made clear in a number of organisms by earlier studies in this series and the comparison of observations on Campanula, Tulipa, Fritillaria, and Stenobothrus has shown us how to analyse the changes undergone by chiasmata in terminalization and has enabled us to define the forces at work in producing these changes (Darlington and Dark, 1932). Hence it is now possible to recognise from typical metaphase conditions of other organisms what the prophase conditions preceding and determining them must have been. This method can be satisfactorily applied to many species in which the prophase is not amenable to direct study.

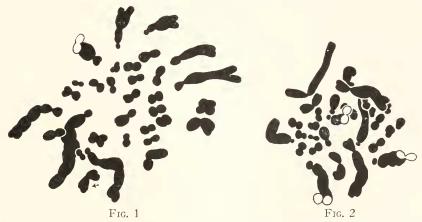
A number of species of plants and animals are known with an extreme range in the sizes of their chromosomes (cf. Darlington, 1932). In species with slight size range the number of chiasmata formed is as a rule roughly proportionate to the lengths of the chromosomes at pachytene (e.g., in Hyacinthus orientalis, Fritillaria imperialis, and Vicia Faba). This would only be possible with a great range of size if the longer chromosomes had a very high number, for the shortest must always form one chiasma, according to the chiasma theory of pairing, to ensure that they pair regularly (Darlington, 1930).

The indirect size-frequency relation expected on this theory has been found in *Stenobothrus* and *Chorthippus* where the extreme lengths are as 8 to 1. It may be inferred on the analogy of the observations in *Brachystola, Yucca flaccida* (O'Mara, 1931), and in the South American Acrididæ (Saez, 1930). In the last the abnormal frequency relation is evidently due to localization of chiasmata near the spindle attachment so that the same length of chromosome is concerned in forming chiasmata in all the chromosomes. In the other examples the distribution is even and the mechanism controlling the abnormal length-frequency relation cannot be so directly inferred.

High size ranges occur in many species of monocotyledons. In Eucomis bicolor, 2n = 32 (Fig. 1) (cf. Müller, 1912), and in Hyacin-

thus amethystinus,  $2n = 28^{\circ}$  (Fig. 2), the range is about 20 to 1, i.e., the same as in Drosophila melanogaster. It is to be noted that the shortest chromosomes are too small to attain the characteristic chromatid breadth of the species. In Hyacinthus the complement consists of 10 chromosomes about 5  $\mu$  long together with 18 less than 1  $\mu$  long and an average about one-tenth the length of the longer chromosomes.

At the first metaphase of meiosis 14 bivalents are regularly found in Hyacinthus amethystinus. Polar views show the five long pairs with two or three chiasmata (Fig. 3). The detailed structure of the nine short pairs cannot be determined from this aspect. As always, it is necessary to examine bivalents of this size in side view. (This is not



Figs. I and 2. Mitotic metaphases from the root tip.  $\times$  3200. Fig. 1. Eucomis bicolor, 2n = 32.

Fig. 2. Hyacinthus amethystinus, 2n = 28.

yet generally appreciated.) It is then found (Fig. 4) that most have a single terminal chiasma, a few have a single interstitial chiasma and occasionally there is one with two chiasmata. The mean chiasma frequencies of long and short types in this division are 2.4 and 1.1 respectively.

These observations show the closest analogy with Stenobothrus and Chorthippus except that the departure from normal in length-frequency relation is even more pronounced. The degree of terminalization is the same: the terminalization coefficient for the longer chromosomes is .45 in Stenobothrus and .42 in Hyacinthus, for the shorter chromosomes .67 in Stenobothrus and .60 in Hyacinthus. It is therefore evident that the conditions of terminalization are similar in the two instances and that since chiasma frequency is not reduced during prophase in Stenobothrus

<sup>&</sup>lt;sup>1</sup> The somatic chromosome number is given by Heitz (1926) as 24.

it is similarly unaltered in *Hyacinthus*, the only change being a movement of interstitial chiasmata to the ends of the chromosomes.



Figs. 3 and 4. First metaphase of meiosis in *Hyacinthus amethystinus*,  $\times$  3200. The total numbers of chiasmata and numbers terminal are given. Sections cut at 24  $\mu$ .

Fig. 3. Polar view. The structure is only identifiable in the long bivalents.



Fig. 4. Side view, bivalents drawn separately.

### SUMMARY

The longer chromosomes of *Hyacinthus amethystinus* are on the average ten times the bulk of the shorter ones but have only twice as many chiasmata per bivalent. Thus, although the longer chromosomes form only two or three chiasmata, the shortest chromosomes regularly form one chiasma which ensures their regular pairing. This abnormality is characteristic of particular species and, like other variations in chiasma frequency and distribution, it must be genetically controlled. It is therefore to be regarded as an adaptive property.

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